

Notes on the Morphology of Bathynella and  
some Allied Crustacea.

By

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With 14 Text-figures.

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I. INTRODUCTORY.

The recent re-discovery of *Bathynella natans* by P. A. Chappuis (1914a, 1915)<sup>1</sup> throws welcome light on one of the most remarkable of living Crustacea. In the thirty years that had elapsed since its first description by Vejdovský (1882), from two specimens found in a well in Prague, this

<sup>1</sup> The numbers in brackets after names of authors refer to the list of papers on p. 513.

minute form had not been obtained by any other naturalist. Some eighteen years ago a re-examination of the solitary remaining specimen enabled me, in spite of its poor state of preservation, to add some details to Vejdovsky's account, and led me to the conclusion that it was allied to *Anaspides* (Calman, 1899). The scantiness of information regarding it, however, has caused most writers who have had occasion to refer to *Bathynella* in text-books or elsewhere to suspend judgment as to its affinities, and the late Geoffrey Smith (1909) omitted it altogether from his revision of the *Anaspidae*. The detailed account of its structure now provided by Chappuis from the specimens found in Switzerland entirely confirms my earlier conclusions as to its systematic affinities, and enables us to say that *Bathynella* is undoubtedly a degenerate member of the *Syncarida*, a group of *Crustacea* which has persisted from Carboniferous times, and of which the only other living representatives are found in Australia and Tasmania.

Certain features in the morphology of *Bathynella* seem to me, however, to deserve somewhat more detailed consideration than they have yet received, and on this account I was particularly glad to have an opportunity of studying three specimens that M. Chappuis kindly presented to the British Museum (Natural History). From the small size of the animal and the unusual delicacy of its cuticular covering its investigation presents considerable difficulty, but I have been able in great part to confirm and in some details to amplify Chappuis' account of its external structure. Since his memoir, published in a German periodical, is likely for the present to be difficult of access for many zoologists, it seemed desirable to make the following account somewhat fuller than might otherwise have been necessary.

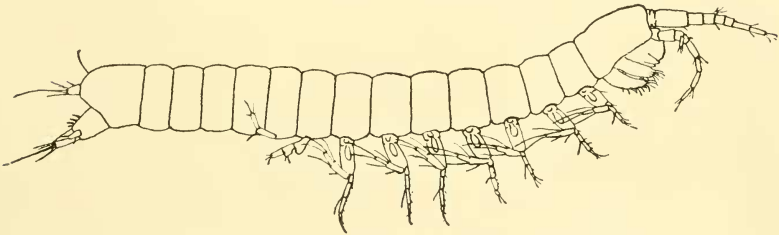
## II. EXTERNAL CHARACTERS OF BATHYNELLA.

Size.—The specimens examined by me measure almost exactly 1 mm. in length of body, and this is also the size

given by Vejdovský for the type-specimens. Chappuis states that some of his specimens reached a length of 2 mm., but it is not quite clear that this measurement excludes the antennules. In any case *Bathynella* is one of the smallest among the Malacostraca; only some Asellota and Cumacea are no larger, and a few Tanaidæ are perhaps even a little smaller.

Body.—The body (Text-fig. 1) is subcylindrical and fully segmented, and the general aspect of the animal approaches that of the more vermiform of the Harpacticoid Copepoda. The abdomen appears to be a little more bulky than the

TEXT-FIG. 1.

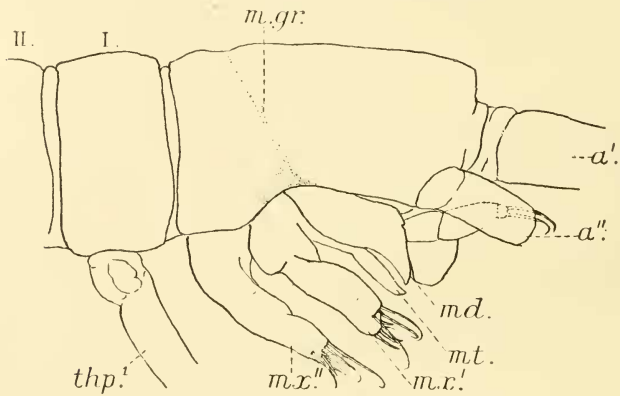
*Bathynella natans*, ♂. Lateral view.

thorax, and, according to Chappuis, it is slightly compressed from side to side. The eight thoracic and six abdominal somites are separated by well-marked grooves and appear to be freely movable, but the cuticle is almost uniformly thin, and there is difficulty in seeing the boundaries between the tergal sclerites and the articular membranes connecting them. The tergites of the posterior thoracic and the abdominal somites overlap from before backwards, but in the anterior three or four thoracic somites there is no overlapping.

Head.—The head (Text-figs. 2 and 3) is longer than wide. It is truncated in front, with no trace of a rostral projection, and behind it is sharply defined from the first thoracic somite by an articulation exactly like those that separate the thoracic somites from one another. There is no trace of eyes or of

eye-stalks. Seen from the side, the lower margin is concave in its anterior two-thirds, and in this part it overhangs the bases of the mandibles and maxillulae in a very slight pleural fold. On the side of the head a shallow groove, most clearly seen in a specimen treated with caustic potash, runs obliquely upwards and backwards, becoming almost imperceptible where it joins with its fellow across the dorsal surface. At its lower end, where it lies immediately above the basal articulation of the mandible, the integument along the floor of the

TEXT-FIG. 2.



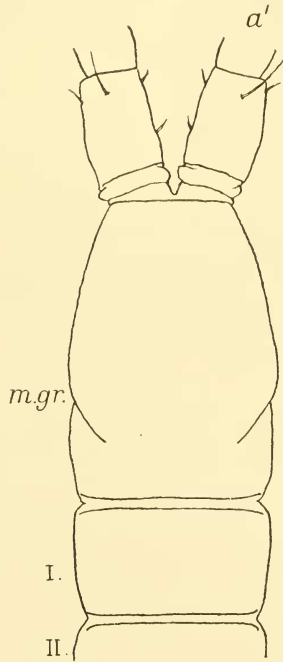
*Bathynella natans*, ♀. Head and anterior thoracic somites, lateral view. *a'*. Base of antennule. *a''*. Base of antenna. *md.* Mandible. *m.gr.* Mandibular groove. *mt.* Metastoma or lower lip. *mx'*. Maxillula. *mx''*. maxilla. *thp¹*. Appendage of first thoracic somite. I, II. Tergites of first and second thoracic somites.

groove is slightly thickened and stiffened, and this thickening spreads a little way in front and behind along the margin of the pleural fold. The significance of this "mandibular groove" is discussed below.

Telson.—The sixth abdominal somite is deeply incised behind in the middle line where the anus opens, and on either side of the incision, towards the dorsal side, a short appendage is articulated, subcylindrical or slightly flattened, and

bearing a group of spines and long setæ (Text-figs. 4 and 5). These appendages are not divided into two segments as Vejdoický described them, and one of the grounds for my suggestion that they might represent the caudal furca is therefore removed. I am now inclined to agree with

TEXT-FIG. 3.



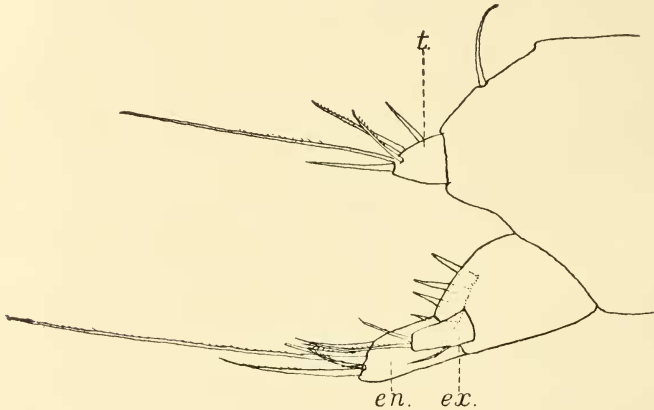
*Bathynella natans*, ♀. Head and anterior thoracic somites, dorsal view. *a'*. Base of antennule. *m. gr.* Mandibular groove. I, II. First and second thoracic somites.

Chappuis that they represent the two halves of a deeply divided telson, although I do not understand his argument when he says—"Da aber das Analsegment hier schon die Uropoden trägt, so ist die Deutung der 2 Schwanzplatten als Furcalglieder ausgeschlossen." In no other Syncarida does the telson show even a tendency to division, and although in

many Gammaridea the telson is split almost or quite to the base, the two parts are never set wide apart as they are in *Bathynella*.

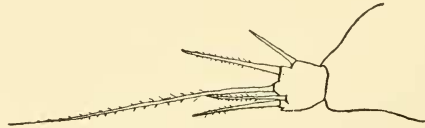
Antennule.—The earlier accounts described the an-

TEXT-FIG. 4.



*Bathynella natans*, ♀. Last somite, telson, and uropod, lateral view. *en.*, *ex.* Endopodite and exopodite of uropod. *t.* One of the telson-plates.

TEXT-FIG. 5.



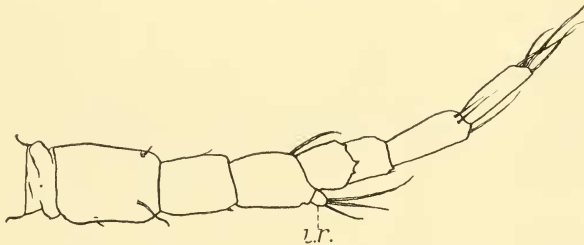
*Bathynella natans*, ♀. Telson-plate of right side, dorsal view.

tennule as uniramous, but Chappuis has discovered that a minute vestige of the inner ramus persists. According to his interpretation this vestige is attached to the distal end of the fifth segment. If this be so, it constitutes a very remarkable exception to the rule that the peduncle of the antennule in the Eumalacostraca consists of three segments. This rule is only infringed, as far as I know, in certain species of

Apseudes, where, according to Claus, the rami are coalesced at the base so as to form an apparent fourth segment of the peduncle. In the Phyllocarida the peduncle consists of four segments.

At first sight, the antennule of *Bathynella* (Text-fig. 6) seems to bear out Chappuis' description. On the proximal side of the vestigial inner ramus it presents three large segments following upon two extremely short basal segments, the latter together representing the first segment as figured by Vejdovský. A careful examination of these short seg-

TEXT-FIG. 6.



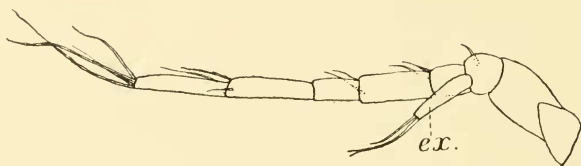
*Bathynella natans*, ♀. Antennule of left side, dorsal view.  
 Drawn from a cleared specimen in which some of the finer setæ are missing. *i. r.* Vestige of inner ramus.

ments, however, leaves some doubt as to their being real segments of the peduncle (Text-figs. 2, 3, and 6). The proximal of the two forms a ring of chitin, not defined from the exoskeleton of the head by any articulation or line of suture, although it is overlapped above by a slight fold forming the frontal margin of the cephalic tergite. It may well be that this apparent proximal segment is simply the everted margin of the socket with which the antennule articulates. The second segment has a less firm outline than the first and the succeeding segments; its surface (in the single specimen in which I examined it closely) was irregularly folded and wrinkled, and it may be nothing more than the articular membrane of a joint that has more than the usual range of motion. At all events there appears to be no

reason for attributing any profound morphological significance to these supernumerary segments of the peduncle.

*Antenna*.—Chappuis points out that the peduncle consists of three segments, a short basal segment preceding the two figured by Vejdovský. In this case there can be no question that Chappuis' observation is correct, the additional segment being well defined both proximally and distally (Text-fig. 7). The character is possibly of importance, since in the other living Syncarida, as in most Malacostraca, only two segments are present. In this respect *Bathynella* agrees with the Mysidacea and many other Peracarida. The third segment

TEXT-FIG. 7.



*Bathynella natans*, ♀. Antenna of left side, dorsal view.

bears a small unsegmented exopodite tipped with two setæ, and is followed by a flagellum of five elongated segments.

*Mouth-parts*.—The mandible (Text-fig. 8, *md.*) has a palp of three segments, of which the second is much the longest. The oral edge is irregularly toothed, and its proximal part, which would correspond to the molar process, is thin and sharp-edged. The lower lip (Text-fig. 2, *mt.*) is large, as in other Syncarida, and its lobes appear to terminate each in a minute inturned point.

The maxillula (Text-fig. 8, *mx.*) is incorrectly figured by Chappuis. It has two endites, the proximal small and bearing two apical setæ, the distal armed with a group of spines. A rounded distal eminence on the outer side, bearing three setæ, no doubt represents a vestigial palp. The whole appendage bears an unmistakable resemblance to that of *Koonunga* as figured by Sayce (1908, Pl. I, fig. 12). No

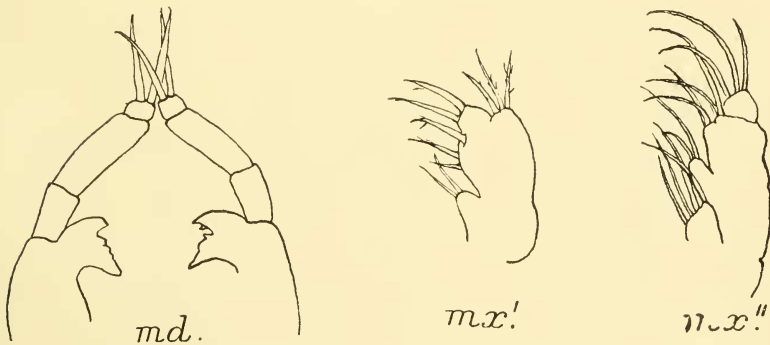


trace can be detected of the exite which is present in *Anaspides*.

The maxilla (Text-fig. 8, *mx.*"') has three endites and a short unsegmented palp. Here also a certain resemblance to *Koonunga* may be traced in the fact that the endites are directed inwards, and not crowded together as they are in *Anaspides*.

Thoracic Appendages (Text-figs. 9 and 10).—With exception of the last pair all the thoracic limbs are similarly

TEXT-FIG. 8.



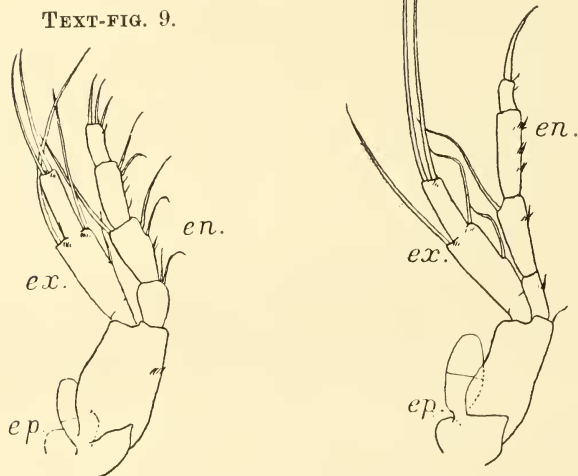
*Bathynella natans*, ♀. *md.* Mandibles. *mx'*. Maxillula.  
*mx''*. Maxilla.

constructed, only the inner ramus becoming a little longer and more slender in passing backwards along the series, and the group of spines arming the terminal segment being reduced to a single claw (with a minute seta at its base) in the last three pairs. The coxopodite is short, and has two vesicular epipodites on its outer surface. The basipodite is long, and both exopodite and endopodite articulate with its distal end. The exopodite shows an incomplete line of articulation near the base and another beyond the middle of its length, where there is a well-marked "shoulder" on each side; it is not, however, distinctly divided into two segments as described by Vejdovský and myself. The endopodite consists of four segments, the precise relation of which to the

six segments present in *Anaspides* cannot be determined. From the fact that the exopodite is attached to the distal end of the second segment of the protopodite it may be inferred that this segment represents the basipodite alone, and not the coalesced basipodite and ischiopodite as it does in *Koonunga* and in the posterior legs of *Anaspides*.

The appendages of the last thoracic somite are greatly

TEXT-FIG. 10.



TEXT-FIG. 9.

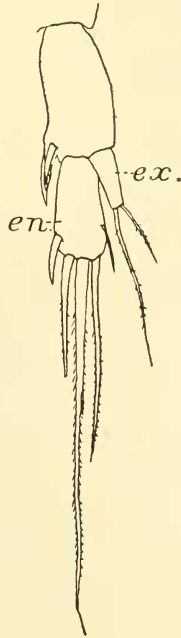
FIG. 9.—*Bathynella natans*, ♀. Thoracic appendage of third pair.  
*en.* Endopodite. *ep.* Epipodites. *ex.* Exopodite.

FIG. 10.—*Bathynella natans*, ♀. Thoracic appendage of sixth pair.  
References as in Text-fig. 9.

reduced in size, and differ considerably in structure in the two sexes. In the female the exopodite and endopodite are short, unsegmented stumps, and a single epipodite is present. In the male (Text-fig. 1) the exopodite is reduced to a papilla, there is no epipodite, and the coxopodite is produced internally as a rounded prominence on which, or at any rate very near it, is the opening of the vas deferens.

While Vejdovský and I had only described a single series of thoracic epipodites, Chappuis has made the important discovery that *Bathynella*, like all other living Syncarida, possesses a double series of these appendages. The distal epipodites are oval vesicles (not flattened, at least in pre-

TEXT-FIG. 11.



*Bathynella natans*, ♀. Uropod of right side, dorsal view.  
*en.* Endopodite. *ex.* Exopodite.

served specimens) attached to the proximal segment of the limb by a narrow base. Chappuis does not describe them as showing any structural differentiation, but in a cleared specimen each is seen to be crossed by a fine suture-line about the middle of its length. In the distal half of the vesicle the cuticle is slightly thickened, forming a thimble-shaped cap, while the proximal part has the cuticle thin and flaccid. I formerly described the epipodite as "borne on a

short peduncle, from which it is separated by a transverse articulation or suture." It now appears probable that the "peduncle" was formed by the collapse of the proximal part of the epipodite in the shrivelled type-specimen. In reality there is no peduncle, the epipodite springing directly from a narrow base of attachment. The transverse suture suggests comparison with the suture-line which I described near the base of the epipodites of *Anaspides*, but in that case it is the small basal portion which is more thickened, and the distal part soft and membranous.

The epipodites of the proximal series are not constricted at the base, but form merely lobular processes of the outer surfaces of the coxopodites. They have a very delicate cuticular covering and are not divided by suture.

Abdominal Appendages.—In the abdominal region the only appendages present are those of the first and sixth somites. The former (pleopods) are short, uniramous, and consist of two segments; they present no sexual differences (Text-fig. 1). The appendages of the sixth somite (uropods) (Text-figs. 4 and 11) are very stout, with the peduncle laterally compressed, and armed with a row of spines on the inner side; the endopodite is subcylindrical, and bears a group of spines and long setæ distally; the exopodite is conical, much shorter than the endopodite, with two apical setæ.

### III. INTERNAL ANATOMY OF BATHYNELLA.

As I have had no opportunity of studying the soft parts, the following notes are based solely on the observations recorded by Chappuis.

Alimentary System.—No masticatory stomach is described, a smooth muscular œsophagus extending as far as the sixth thoracic somite. This is followed by a widened portion ("Magen") reaching into the last thoracic somite, with opaque glandular walls thrown into four longitudinal folds. This may be supposed to represent at least a portion of the

mid-gut, although Chappuis applies that name to the following, still wider portion, which extends as far as the fourth abdominal somite. In this region the dorsal wall of the gut is thick and glandular, while the ventral wall is thin. The short rectum is stated also to have a glandular structure.

The entire absence of hepatic or other diverticula of the gut is a feature not paralleled in any other Malacostracan.

**Circulatory System.**—The short heart lies in the fourth thoracic somite, and does not exceed in diameter the vessels that come off from it in the middle line in front and behind. No ostia have been seen. While the anterior vessel is no doubt an aorta (*arteria dorsalis*, Chappuis), the posterior vessel is described as a “*vena dorsalis*” collecting the blood from the sixth abdominal somite and returning it to the heart. Such an arrangement would be very unusual, if not unique, among Crustacea, and perhaps the so-called dorsal vein should be regarded rather as a backward extension of the heart itself. In view, however, of the difficulties of investigation to which Chappuis alludes, it seems possible that a mistake has been made as to the direction of the blood-flow in this region of the body.

**Excretory System.**—Chappuis describes in considerable detail the remarkable structure of the maxillary gland. It consists of an end-sac (*cœlomic sac*), a looped canal extending backwards into the fourth thoracic somite, and a terminal vesicle with a slit-like opening on the outer surface of the maxilla. During life the terminal vesicle is thrown into rapid pulsation, with opening and shutting of its external aperture, by a muscle attached to its wall. This pulsating apparatus is compared by Chappuis with that found in the maxillary gland of the remarkable Copepod *Phyllognathopus* (*Belisarius*, *Viguiereella*), where it was first described by Maupas, and has recently been investigated by Chappuis himself (1914b) in specimens found living in company with *Bathynella*. The similarity, however, appears to be no more than superficial, either in structure or, probably, in function, for while the pulsating vesicle of *Bathynella* is

situated at the exit from the excretory duct, that of *Phyllognathopus* is at its inner termination, and represents, in all likelihood, a modification of the coelomic sac.

An excretory function is also ascribed to paired nephrocytes, or masses of them, in the head and body-somites, and in the same connection there is described a pair of voluminous glandular masses in the last somite, with ducts opening on the uropods.

**Nervous System.**—The central nervous system is remarkably bulky in comparison with the other organs. The large brain shows no trace of optic lobes. The ventral nerve-chain shows some degree of longitudinal concentration (not very fully described), and the ganglia are indistinctly defined from the connectives.

**Reproductive System.**—The reproductive system of both sexes is simple. The gonads lie in the abdomen, and their ducts run forwards to open to the exterior in the positions characteristic of the Malacostraca, those of the female on the sixth and those of the male on the eighth thoracic somite.

#### IV. DEVELOPMENT OF BATHYNELLA.

The only young stage observed by Chappuis (the size is not stated) resembled the adult, except that the last four pairs of thoracic limbs were rudimentary. The single pair of pleopods and the uropods were fully developed. This is in curious contrast to *Koonunga*, the only other Syncaridan of whose development we know anything, where Sayce (1908, p. 11) found a young specimen with all the thoracic appendages fully developed while the pleopods were still unsegmented buds.

#### V. THE FIRST THORACIC SOMITE IN THE SYNCARIDA AND OTHER MALACOSTRACA.

In discussing the structure of *Bathynella* in 1899 I pointed out that it possessed eight free somites in the

thoracic region instead of seven as described by Vejdovský. This conclusion is fully confirmed by Chappuis and the character is so unusual that it deserves further consideration.

I formerly stated (1899, p. 342) that "Nebalia and some Stomatopods" agreed with *Bathynella* in having the first thoracic somite free from the head. As regards the Stomatopoda, this statement was based on a remark of Claus,<sup>1</sup> which appears to be true only of the larvæ. No adult Stomatopod has the tergites of the first or second thoracic somites free from the carapace, while those of the third and fourth are only indistinctly represented.<sup>2</sup>

In *Nebalia*, the carapace envelops, but remains free from, the thoracic tergites. The grooves separating these from one another are distinct, but the anterior limit of the first tergite coincides with the line along which the free carapace passes into the dorsal integument of the head-region, and it is not possible to say that the first tergite is defined from the head in the same way as it is from the following tergite. Owing to the small size of *Nebalia* it is difficult to obtain a clear view of the parts in question, but it is comparatively easy to do so in the case of the large Mysidacea of the genus *Gnathophausia*, in which also the first thoracic somite has been stated to be distinct from the head.<sup>3</sup>

If the free portion of the carapace be cut away on one side of a specimen of *Gnathophausia* (Text-fig. 12) the tergites

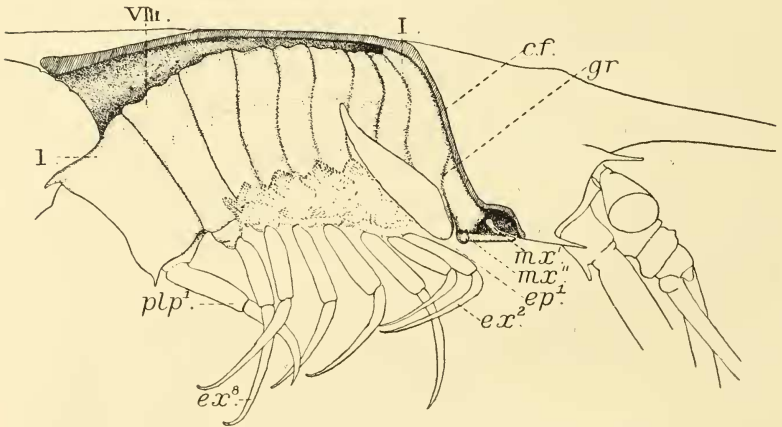
<sup>1</sup> "Bei den Squilliden bleibt übrigens die ganze Region der Kieferfüsse vom Rückenschilde getrennt, das Segment des ersten Kieferfusses geht hier unterhalb der Schildplatte in die Innenlamelle über" (Claus, 1876, p. 53).

<sup>2</sup> Giesbrecht (1910, p. 9, pl. ii, fig. 9) states that the structures here regarded as the tergites of the third and fourth somites represent respectively the tergites of the first and second and of the third and fourth somites fused together, but it is not clear on what evidence this statement is based.

<sup>3</sup> "In Sars' figure of *Gnathophausia longispina* . . . the first thoracic segment appears to be limited in front by a definite groove, which would thus separate the cephalic and thoracic regions" (Lister, 1909, p. 436, footnote).

of the thoracic somites are easily seen. The investing cuticle, however, is almost uniformly thin, and the tergites, which are hardly to be described as sclerites, are defined from one another only by superficial grooves. In the posterior part of the thoracic region the tergites are regularly transverse, but anteriorly the median portions are pushed backwards and crowded together owing to the backward extension of the connection between the carapace and the body, which extension is visible externally on the dorsal surface of the carapace

TEXT-FIG. 12.



Gnathophausia zoea. Anterior region of body with free portion of carapace cut away, from right side. *c.f.* Origin of carapace-fold. *ep*<sup>1</sup>. Epipodite of first thoracic appendage (maxilliped). *ex*<sup>2</sup>, *ex*<sup>3</sup>. Exopodites of second and eighth thoracic appendages (that of the first is absent in this species). *gr.* Groove marking boundary between maxillary and first thoracic somites, uniting above with origin of carapace-fold. *mx*<sup>1</sup>. Palp of maxillula. *mx*<sup>2</sup>. Maxilla. *plp*<sup>1</sup>. Pleopod of first pair. I, VIII. Tergites of first and eighth thoracic somites. I. Tergite of first abdominal somite.

as the "linguiform area" of Sars (1885, p. 22). This crowding makes it difficult to count the narrowed anterior tergites, but by careful manipulation seven of them can be distinctly seen to be continuous across the mid-dorsal line. The foremost of these, the second thoracic tergite, is defined in



front by a well-marked groove from the strip of cuticle which is reflected to become the lining membrane of the carapace. On each side this strip (Text-fig. 12, *I*) widens somewhat and becomes what is clearly the lateral portion of the first thoracic tergite. For the greater part of its length it is limited anteriorly by the fold (Text-fig. 12, *c.f.*) which marks the beginning of the free portion of the carapace. Towards its lower end this fold turns forward to run horizontally where the lateral, or pleural, margin of the carapace overhangs the bases of the mouth-parts and antenna. No considerable part of the lateral wall of the head is exposed between the origin of this pleural fold and the attachment of the appendages except in the case of the maxilla, where a short space intervenes. In front, this space is bounded by a cavity in which lies the palp of the maxillula (Text-fig. 12, *max'*); behind, between the base of the maxilla and that of the first thoracic appendage, a shallow and inconspicuous groove (Text-fig. 12, *gr.*) can be traced running upwards for a little distance and curving forwards to join the carapace-fold. It is this short groove alone that can be definitely stated to mark the boundary between maxillary and first thoracic somites, or, in other words, between head and thorax.

With exception of the short groove just mentioned, which I have not been able to observe in any other form, the conditions found in *Gnathophausia* appear to be repeated in all those cases where the eight thoracic tergites have been stated to be free from the enveloping carapace (*Nebalia*, larval Stomatopods, larval Decapods); that is to say, the cephalothoracic tergal boundary is coincident with, and is obscured by, the origin of the carapace-fold. Further, since there is reason to believe that where the first thoracic somite is coalesced with the head, as it is in Isopoda and Amphipoda, a vestigial carapace-fold is involved in the coalescence, we arrive at the conclusion that *Bathynella* and the Anostracous Branchiopoda are the only living Crustacea<sup>1</sup> in

<sup>1</sup> Possibly the Copepoda should be added, but the case is a little obscure (cf. Calman, 1909, pp. 6 and 73).

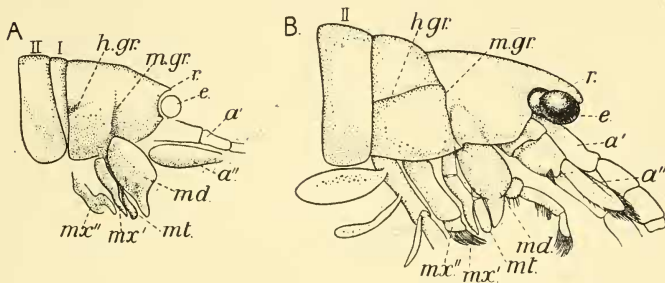
which the carapace is entirely absent. It is this that gives special importance to the agreement between *Bathynella* and some of the genera of fossil Syncarida (*Uronectes*, *Palaeocaris*) in which the first thoracic somite is similarly free from the head.

#### VI. THE MANDIBULAR GROOVE IN THE SYNCARIDA.

*Anaspides* was originally stated to have, as *Bathynella* has, eight free thoracic somites, but I pointed out in 1896 that the supposed first thoracic somite was defined from the head not by a movable articulation like those between the following somites, but by a superficial groove in the integument, and that this groove, from its position immediately behind the mandibles, probably did not mark the cephalothoracic boundary.<sup>1</sup> I later expressed some uncertainty as to this interpretation, but it was strongly confirmed by the discovery that in the fossil genus *Palaeocaris* (Text-fig. 13, *A*) where eight free thoracic somites are clearly defined, a short groove is present on the side of the head, running upwards from the base of the mandible in exactly the same position as the more strongly marked groove of *Anaspides* (Calman, 1911, p. 489). To this groove, thus shown to have nothing to do with the first thoracic somite, the name of "mandibular groove" (Text-fig. 13, *m. gr.*) was given, and it is of particular interest to find it present also in *Bathynella*. In this genus the groove, although no more conspicuous than it is in *Koonunga* (Text-fig. 14) has the same relative position as, and is undoubtedly homologous with, that

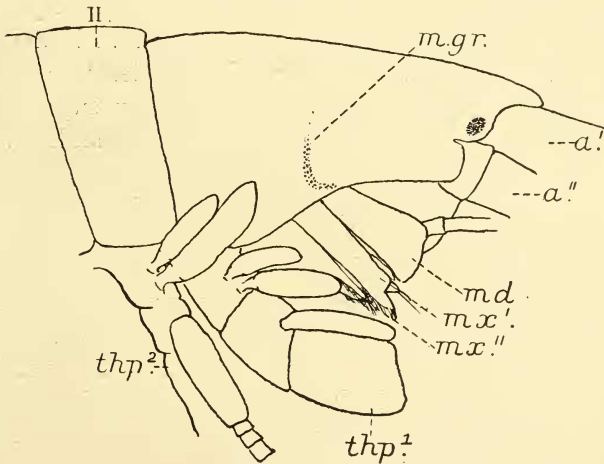
<sup>1</sup> The "faint impressed line" described (Calman, 1896, p. 788) as running behind the mandibular groove in *Anaspides* is very ill-defined and inconstant, and no morphological significance can be attributed to it. The "horizontal groove" is not so deep or so sharply marked as the mandibular; it is still shallower in *Paranaspides*, and in *Koonunga* I can only see a doubtful trace of it. It is associated with a bulging of the side wall of the head in this region (shown, for instance, in Sayce's figures of *Koonunga*), which apparently marks the position of the maxillary gland.

TEXT-FIG. 13.



Head and anterior thoracic somites, lateral view. A *Palaeocaris præcursor* (fossil, Coal-measures). B *Anaspides tasmaniae*. *a'*. Antennule. *a''*. Antenna. *e*. Eye. *h. gr.* Horizontal groove. *md.* Mandible. *m. gr.* Mandibular groove. *mt.* Metastoma or lower lip. *mx'*. Maxillula. *mx''*. Maxilla. *r.* Rostrum. I, II. Tergites of first and second thoracic somites. (From 'Geol. Mag.,' 1911, by kind permission of the editor.)

TEXT-FIG. 14.



*Koonunga cursor*. Head and anterior thoracic somites, lateral view. *a'*. Base of antennule. *a''*. Base of antenna. *md.* Mandible. *m. gr.* Mandibular groove. *mx'*. Maxillula. *mx''*. Maxilla. *thp<sup>1</sup>*, *thp<sup>2</sup>*. Appendages of first and second thoracic somites. II. Tergite of second thoracic somite.

of Anaspides; while, as in Palæocaris, it co-exists with a clear demarcation between the head and the first thoracic somite. As was previously pointed out this mandibular groove is, in all probability, to be identified with that named by Sars "cervical sulcus" in the Mysidacea, with the transverse cephalic groove of the Anostraca and Conchostraca, and with the anterior transverse groove of the carapace in Apus and other Notostraca. It is possible, but much less certain, that it corresponds to a part at least of the "anterior cervical groove" of Decapoda. As regards its morphological significance, its position at the limit between the naupliar and post-naupliar regions of the body suggests that it may be of great phylogenetic antiquity and importance. It is quite possible, however, that it may have rather a mechanical and functional meaning. In the Anostraca the bottom of the groove is thickened to form a more or less continuous chitinous bar connecting across the dorsal surface of the head the points of articulation of the two mandibles. The thickening is most marked, as it is in *Bathynella*, at the ends of the groove; and there can be little doubt that, whatever its origin, this groove has, at least in these two cases, the function of giving the necessary support for the articulation of the proximal condyle of the mandible.

#### VII. THE DEGENERACY OF BATHYNELLA.

The structure of *Bathynella*, as compared with that of its immediate allies, is obviously, in many respects, simplified or degenerate. Some of the evidences of degeneration are no doubt correlated with the habitat of the animal, particularly the absence of eyes, which is almost universal in animals that inhabit subterranean waters. It is quite likely, however, that the simplification of structure is in great part a direct consequence of unusually small size. Lankester (1880, p. 51) long ago pointed out that "the needs of a minute animal are limited as compared with those of a large one," and he enumerated as one of the causes of degeneration "excessive

reduction of size." Thus, we may suppose that the absence of diverticula of the alimentary canal and the reduction of the epipodial vesicles in *Bathynella* are due to the fact that the necessary proportion of secretory, absorptive, and respiratory surfaces can be attained without the need for out-growths that are indispensable for more bulky organisms. Apart from questions of adaptation, however, there are other ways in which size greatly influences structure. As D'Arcy Thompson (1917, p. 33) has recently reminded us, the physical and mechanical conditions of growth may be profoundly different in a small animal from what they are in a large one. For example, we find in *Bathynella* and, I believe, in all minute Crustacea, a certain clumsiness of modelling and a tendency to rounded outlines in the smaller appendages such as the mouth-parts which may be the result of the greatly increased pressure due to surface tension on strongly curved surfaces. With regard to some other characters we can only dimly guess at the mechanical principles that may be involved. It seems to be a general rule, to which *Bathynella* conforms, that in small Crustacea the setæ on the limbs are fewer in number and larger in relative size than in larger species. It is rare, in very small Crustacea, to find any of the appendages produced into long multiarticulate flagella. Where such flagella are present, as in the antennæ of the males of some Cumacea hardly larger than *Bathynella*, the segments of which they are composed are always much longer than wide. So, in the antennules and antennæ and in the thoracic exopodites of *Bathynella*, the small number of segments and their elongate form are very striking when compared with the same appendages of *Anaspides*.

#### VIII. THE CLASSIFICATION OF THE SYNCARIDA.

If we compare the characters of the living genera of Syncarida it is at once apparent that *Anaspides* and *Paranaspides* are closely related, while *Koonunga* and *Bathynella* differ widely from them and from one another.

There can, therefore, be no question as to the desirability of recognising the three families Anaspididæ, Koonungidæ, and Bathynellidæ. When, however, we attempt to define more closely the relationships between these families, and especially when we try to frame a scheme of classification to include the fossil genera as well, the matter becomes much more complicated.

The attractive simplicity of a dichotomous classification is always less easy to escape from and more likely to be misleading when the forms to be classified are few and the characters available for their discrimination are scanty. Such dichotomies have more than once proved a snare to the taxonomist of Crustacea<sup>1</sup> and they have already made their appearance in the attempts to classify the Syncarida. Thus Chappuis, in his preliminary paper on *Bathynella* (1914A, p. 47) proposed to divide the members of the group into Pleopodophora and Apleopodophora<sup>2</sup> according as they possess a full or a reduced series of abdominal appendages. In his later paper (1915, p. 172) at my suggestion, he based his division on the freedom or coalescence of the first thoracic somite, naming the groups Bathynellacea and Anaspidacea. Still more recently Vanhöffen (1916)<sup>3</sup> has separated the genera that possess thoracic exopodites from the fossil genera in which these appendages have not yet been discovered, opposing the new name Duplicipoda to Fritsch's Simplicipoda. It would be difficult, perhaps, to find a basis of classification with less to commend it than that selected by Dr. Vanhöffen.

<sup>1</sup> We need only recall the false antitheses of Entomostraca and Malacostraca, Phyllopora and Cladocera, Edriophthalma and Podophthalma, Macrura and Brachyura. In each of these cases one of the paired groups has proved, on closer examination, to be a heterogeneous assemblage.

<sup>2</sup> Giving, by accident or by design, to the division that excludes *Bathynella* the group-name originally devised by Vejdovský (1899) for *Bathynella* alone.

<sup>3</sup> I am again indebted to M. Chappuis for the loan of Dr. Vanhöffen's pamphlet.

I am still of opinion, for the reasons given above, that the freedom of the first thoracic somite is the most weighty morphological distinction between *Bathynella* and the other living *Syncarida*, and that it constitutes an important link between that genus and the fossil *Uronectes* and *Palæocaris*; but so long as this evidence of affinity remains unsupported by other characters I am doubtful as to the desirability of establishing a new sub-order for these three genera. It seems better to be content with a division of the *Syncarida* (or *Anaspidacea*) directly into families, following in this the example of Geoffrey Smith, although both the definitions and the contents of the families recognised by him require modification. Several of the fossil genera, such as *Nectotelson*, *Palæorchestia*, and *Gasocaris*, are so imperfectly known that it is impossible to be sure of their place in any system. *Præanaspidēs*, included by Geoffrey Smith in the family *Anaspididæ*, has proved (Calman, 1911) to be identical with *Palæocaris* which he placed in the *Gampsonychidæ*, although evidently suspecting that the two genera might be more closely related. With some changes in nomenclature recently made by Cockerell, the classification now stands as follows:

Division *Syncarida*, Packard, 1885.

Order *Anaspidacea*, Calman, 1904.

Family *Anaspididæ* (*Anaspidæ*, Thomson, 1893).

Genera *Anaspidēs*, Thomson; *Paranaspidēs*,  
G. Smith.

Family *Koonungidæ*, Sayce, 1907.

Genus *Koonunga*, Sayce.

Family *Acanthotelsonidæ*, Cockerell, 1916  
(= *Pleurocaridæ*, Chappuis, 1915).

Genera *Acanthotelson*, Meek and Worthen;  
*Pleurocaris*, Calman.

Family *Bathynellidæ*, Grobben, 1904.

Genus *Bathynella*, Vejdovský.

Family *Uronectidæ*, Cockerell, 1916 (= *Gampsonychidæ*, Packard, 1885).

Genera *Uronectes*, Bronn (= *Gampsonyx*, Jordan nec Vigors = *Gampsonychus*, Burmeister); *Palæocaris*, Meek and Worthen (= *Præanaspides*, H. Woodward).

#### IX. THE AFFINITIES OF THE SYNCARIDA.

While the investigation of *Bathynella* throws little further light on the systematic relations of the Syncarida as a whole, a few comments may be made here on some opinions recently expressed on the subject. Geoffrey Smith, accepting the general scheme of classification adopted by me for the Malacostraca, regarded the Syncarida as standing near the direct line of descent of both Eucarida and Peracarida. He assumed, however, that the carapace, possessed by the primitive Eumalacostraca, was lost in the common ancestor of all three groups, and redeveloped independently by the Mysidacea on the one hand and by the Eucarida on the other. This assumption is not only improbable, but unnecessary. In the Carboniferous period there existed a considerable variety of Malacostraca, regarding which we know little more than that they possessed a carapace and the other characters of the "caridoid facies." It is not at all unlikely that some of these may have possessed all the characters that, in the Syncarida, we regard as primitive, and that from them may have been derived, by separate and diverging lines of descent, the present-day Syncarida, Peracarida, Eucarida, and Hoplocarida.

Other authors who have discussed the systematic position of *Anaspides* and its allies have been misled by the traditional classification of the Malacostraca into Podophthalma and Edriophthalma (or Thoracostraca and Arthrostraca), and have been unable to get rid of the idea that the group was in some way related to the "sessile-eyed" Crustacea. Thus Grobben (1904) places his group Anomostraca (a name that has no sort of claim to supersede Packard's Syncarida)



between Thoracostraca and Arthrostraca,<sup>1</sup> while Giesbrecht (1913) even goes so far as to include it as one of the divisions of the Arthrostraca. It may be worth while, therefore, to point out once again that the edriophthalmate orders are unmistakably linked, through the Apsseudidæ and Cumacea, with the lower Mysidacea (Lophogastridæ), and that in this series there is nowhere a place for the Syncarida. This affiliation rests on the evidence, not of one, but of a number of independent characters, which need not be recapitulated here, but which are in no way disposed of by Giesbrecht's bold assumption that the brood-pouch has been independently developed in Mysidacea, Cumacea, and Arthrostraca. As a matter of fact, although the Syncarida evidently form by themselves a division of equal rank with the Eucarida and Peracarida, the balance of characters inclines to ally them rather more closely with the former than with the latter.

#### X. LIST OF PAPERS REFERRED TO.

- Calman, W. T. (1896).—"On the Genus *Anaspides* and its Affinities with certain Fossil Crustacea," 'Trans. Roy. Soc., Edinburgh,' xxxviii, pp. 787-802, 2 pls.
- (1899).—"On the Characters of the Crustacean Genus *Bathynella*," 'Vejdovský,' 'Journ. Linn. Soc. Zool., xxvii, pp. 338-344, pl. xx.
- (1909). "Crustacea." In: 'A Treatise on Zoology,' edited by Sir Ray Lankester, pt. vii, fasc. 3.
- (1911).—"On some Crustacea of the Division Syncarida from the English Coal-measures," 'Geol. Mag.' (dec. v), viii, pp. 488-495, 5 text-figs.
- Chappuis, P. A. (1914A).—"Ueber die systematische Stellung von *Bathynella natans* Vejd.," 'Zool. Anz., xlv, pp. 45-47, 1 text-fig.

<sup>1</sup> Vanhöffen (1916) adopts Grobben's classification, but adds the remarkable opinion "dass die Ordnung [Anomostraca] keine natürliche ist, dass wohl ähnliche, aber nicht wirkliche nahe verwandte Formen in ihr vereinigt wurden."

- Chappuis, P. A. (1914 B).—“Ueber das Excretionsorgan von *Phyllognathopus vignieri*,” *ibid.*, xlv, pp. 568–572, 4 text-figs.
- (1915).—“*Bathynella natans* und ihre Stellung im System,” ‘Zool. Jahrb. Abth. Syst.’ xl, pp. 147–176, pl. iii, 17 text-figs.
- Claus, C. (1876).—‘Untersuchungen zur Erforschung der genealogischen Grundlage des Crustaceen-Systems.’ 4to, Wien.
- Cockerell, T. D. A. (1916).—“The Uropods of *Acanthotelson stimpsoni*,” ‘Journ. Washington Acad. Sci.’ vi, pp. 234–236, 1 text-fig.
- Giesbrecht, W. (1910).—“Stomatopoden. Erster Thiel,” ‘Fauna u. Flora d. Golfes v. Neapel,’ Monogr. xxxiii.
- (1913).—“Crustacea.” In: ‘Handbuch der Morphologie,’ herausg. v. Arnold Lang,’ iv, pp. 9–252, 356 text-figs.
- Grobben, K. (1904).—‘Lehrbuch d. Zoologie, begründet von C. Claus.’ 7 Aufl., 1ste Hälfte, Marburg.
- Lankester, E. Ray (1880).—‘Degeneration: A Chapter in Darwinism.’ Nature Series, London.
- Lister, J. J. (1909).—“Crustacea.” In: ‘A Student’s Text-book of Zoology,’ by Adam Sedgwick, vol. iii.
- Sars, G. O. (1885).—“Report on the Schizopoda.” ‘Rep. Voy. Challenger, Zool.’ xiii, 228 pp., 38 pls.
- Sayce, O. A. (1908).—“On *Koonunga cursor*, a Remarkable New Type of Malacostracous Crustaceans,” ‘Trans. Linn. Soc. (2) Zool.’ xi, pp. 1–16, pls. i, ii.
- Smith, Geoffrey (1909).—“On the Anaspidaea, Living and Fossil,” ‘Quart. Journ. Mier. Sci.’ 53, pp. 489–578, pls. xi, xii, text-figs.
- Thompson, D’Arcy W. (1917).—‘On Growth and Form,’ Cambridge Press.
- Thomson, G. M. (1894).—“On a Freshwater Schizopod from Tasmania,” ‘Trans. Linn. Soc. (2) Zool.’ vi, pp. 285–303, pls. xxiv–xxvi.
- Vanhöffen, E. (1916).—“Die Anomotraken,” ‘Sitz. Ber. Ges. natf. Fr. Berlin,’ 1916, No. 3, pp. 137–152, 15 text-figs.
- Vejdovský, F. (1882).—‘Thierische Organismen der Brunnenwässer von Prag,’ 4to, Prag.
- (1899).—“Ueber die systematische Stellung des Brunnenkrebse *Bathynella natans*” (Czech), ‘Sitz. Ber. k. böhm. Ges. Wiss. Prag.’ 1898, No. 14.